

A KARYOLOGICAL SURVEY OF LONICERA, I

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RECORDS OF PLANT CHROMOSOME NUMBERS have been accumulating for about sixty years and counts now exist for a very great number of genera (Darlington & Wylie, 1955) of the families of temperate regions at least. For tropical, and for temperate plants from the southern hemisphere, the need for random investigations still exists, but for plants from the northern hemisphere the stage has been reached where the further counting of chromosomes will be most effective and useful when carried out either in conjunction with an intensive biosystematic investigation, or where an attempt is made to deal as comprehensively as possible with a whole genus or similar taxon. The present survey is just such an attempt.

The genus *Lonicera* was selected, not because of its particular cytological interest, but because the Arnold Arboretum possesses an unusually rich collection of its species, cultivars, and other taxa. Furthermore, and this was also significant in the selection of *Lonicera*, the late Alfred Rehder, whose revision of the genus (1903) is still the latest comprehensive account to be published, worked at the Arboretum and studied, handled, collected, and identified many of the accessions still in cultivation there.

CYTOLOGICAL MATERIALS AND METHODS

For chromosome counts at meiosis, and for the observation of chromosome pairing and possible abnormalities of division, buds containing microsporocytes undergoing meiosis were fixed in 3:1 parts of absolute alcohol: glacial acetic acid, and kept under refrigeration. The fixative was changed to 70 per cent alcohol for long storage in cases where material had to be preserved for some time before examination. The pollen mother cells were smeared on a slide in a drop of aceto-carmin, and after slight overstaining, a drop of Hoyer's medium (Alexopoulos & Beneke, 1952) was added, gently mixed with the stain, then covered by the cover slip. When carefully warmed and pressed, the slides were satisfactory for counting and have since kept well.

For mitotic counts, root-tip meristems and dividing cells in young leaves were generally used. This material was treated for one hour in a 0.002 M. aqueous solution of oxyquinoline (Tjio & Levan, 1950), and then fixed for ca. 12 hours in 3:1 alcohol; acetic acid. After hydrolysis in N HCl at 60°C for 25 or 15 minutes, for root-tips and leaves respectively, the material was washed in distilled water and sometimes hardened for 10

* In this survey, the cytological investigations have been carried out by one of us (L.R.), and the complementary taxonomy by the other (P.S.G.).

minutes in 70 per cent alcohol. Best results were obtained by staining in leuco-basic fuchsin, followed by maceration on a slide in diluted acetocarmine. After judicial warming and pressing the slides were made permanent, using the freezing technique of Conger and Fairchild (1953).

Because all counts have been documented, no meristematic cells from the roots of germinating seeds have been used in this investigation. Cuttings of the plants to be studied were rooted instead, and we wish to record our thanks to Alfred J. Fordham for carrying this out.

However, favorably squashed cells from anther walls sometimes permitted the counting of diploid cells while the PMC's were still in early prophase; tapetal cells were excluded because of the frequency of irregular or polyploid divisions that occur in them.

All observations were made with a Zeiss phase microscope.

DOCUMENTATION

Chromosome numbers without adequate documentation are almost without value, and in this investigation herbarium specimens have been preserved from each of the individual plants which has been examined cytologically. Either new material has been collected or the plants have been checked against specimens which already exist in the herbarium, i.e., specimens taken from the same plants on previous occasions. In the Arnold Arboretum each individual plant has its own accession number, and is recorded on a detailed map, so that even if labels are lost or transposed, the various plants can be accurately and positively related, each to its accession number and, through this number, to its identification. An attempt has also been made to ensure that the specimen growing under a particular number is the original plant and not, either the understock of a weak graft, or a bird-sown seedling, perhaps of hybrid origin and exhibiting heterosis, which has taken over and smothered the individual growing in that position in the first instance. This has happened, or was found to be taking place, in one or two cases, and *Lonicera tatarica* and its hybrid, *L. × bella*, are particular culprits.

Documentation of the counts recorded below has been achieved by the preservation of herbarium specimens in the herbarium of cultivated plants at Jamaica Plain (AAH) and by the recording of chromosome numbers on the Arboretum's master set of accession cards. The collectors who have been responsible for making specimens during the two years since this survey commenced are: Sandra Callaway, Madelon Dodd, Susan Kreps, Theodore R. Dudley, and Peter S. Green, whose invaluable help is gratefully acknowledged. Prior to this investigation, specimens of the honeysuckles growing in the Arboretum had been collected by Caroline K. Allen, C. E. Kobuski, F. P. Metcalfe, E. J. Palmer, A. Rehder, and C. S. Sargent and, where their collections coincide with plants which have been examined cytologically, their specimens are cited below. In a few cases the collector's name is not actually given on the herbarium sheet, but, from the handwriting or date, it is assumed that the collector was A. Rehder. The oldest

specimen cited is one collected by C. S. Sargent in 1891 from the same clone of *Lonicera korolkowii* from which the actual type specimen was originally gathered. The clone is still living and its chromosomes have been counted.

In addition to the specimens incorporated in the herbarium at Jamaica Plain, duplicate collections have been made in a large number of cases. These are being distributed to other botanic gardens and arboreta, by way of exchange. In every case great care has been taken to check the identity of the plants reported upon, including a critical investigation of the complex of hybrids surrounding *Lonicera tatarica* and its allies (Green, 1966).

CYTOLOGY

The basic chromosome number of the genus *Lonicera* is nine and the majority of the species studied are diploid. Polyploidy seems to have played a minor role in speciation within the genus, for only a limited number of wild species are known to be tetraploids or hexaploids. However, some varieties and cultivars of diploid species have been found to be polyploid, but not among the many cultivars of Section LONICERA. No triploids have been reported for the genus, although *L. henryi* has been observed as being hexaploid, a condition also recorded for *L. periclymenum* by Gadella and Kliphuis (1963).

The chromosomes are small (from about 1.5μ), but preliminary karyogram studies of mitotic chromosomes show that the nine chromosomes have a definite morphology which enables the observer to distinguish some of them individually, while others are present in small groups of similar size and shape. Also, the overall size of the complement differs between some species, and investigations are in progress to determine whether or not these differences in size or morphology coincide with the infrageneric groupings proposed by Rehder. The results will be recorded in a subsequent paper but, as a preliminary observation, it may be said that in at least one group of related species a pair of chromosomes may be found which bear satellites consistently, while in others they are apparently absent. The satellites may be seen in FIGURE 1 which shows a root tip cell of *Lonicera morrowii* at metaphase and exemplifies the typical morphology of the complement found in *L. tatarica* and its related species.

As indicated below, hybridization between *Lonicera tatarica* and related species takes place very readily, yet, in these cases, no disturbance in the pairing relationships of the chromosomes was generally observed at meiosis, and the hybrids produced are abundantly fertile.

NOMENCLATURE

No attempt has been made to revise the genus *Lonicera*. The nomenclature and sequence of species is that of Rehder (1903), and as modified by him many years later (1949). If chromosome counts have already been recorded under names not recognized in these two publications, the names

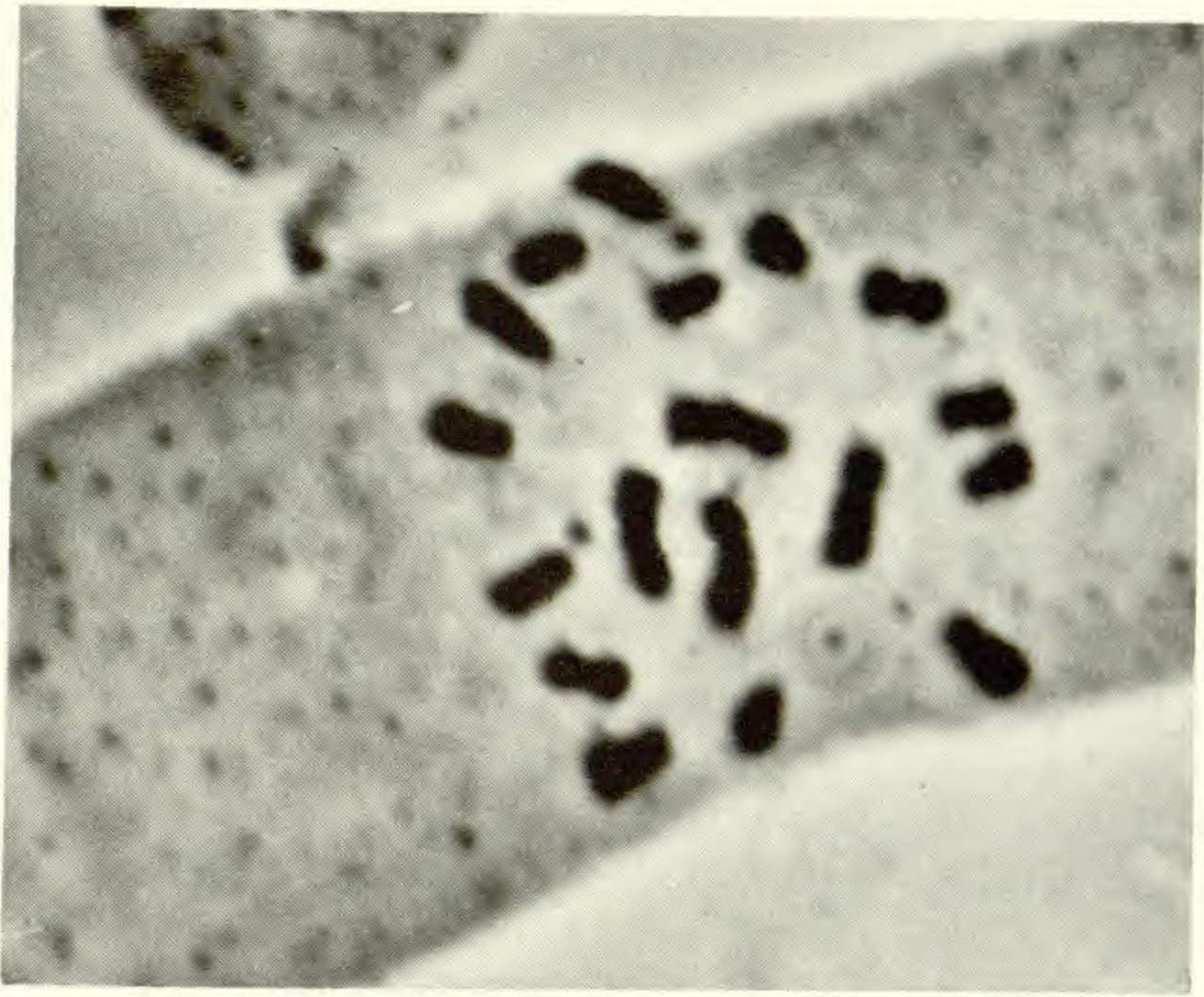


FIGURE 1. Mitotic metaphase in root-tip cell of *Lonicera morrowii* (AA 1283-65); note metacentric chromosomes and a pair with satellites.

are cited in parentheses, otherwise no attempt is made to provide synonymy.

Backcrossed hybrids are listed under their respective hybrid epithet, which is taken to cover all hybrids between the species involved, whether intermediate or backcrossed to either parent.

In accordance with the present International Code of Botanical Nomenclature the names of infrageneric divisions have been modified slightly from those of Rehder. The correct names at subgeneric and sectional level are discussed by Ferguson (1966) whose treatment is followed.

In the case of *Lonicera modesta* and its variety *lushanensis*, both described by Rehder, an examination of the material now available in the herbaria of wild (A) and cultivated (AAH) plants shows that some re-assessment and differentiation is required. Rehder based the differences between the type variety and var. *lushanensis* upon pubescence and leaf-shape. Leaf-shape now appears to be valueless for distinguishing the two, and degree of pubescence is never a very reliable character alone. However, one of the two plants of this species whose chromosomes have been examined in this investigation (both raised from seed sent in 1936 from Lushan Botanic Garden in China) has proved to be diploid and the other tetraploid. The former has densely pubescent stems, and leaves with scattered hairs all over the lower leaf surface, and most nearly approaches the type variety, whereas, the latter has stems glabrous or with only a few hairs, and the leaves almost glabrous. The amount of flowering material available is still inadequate but it is suspected that more reliable morphological characters for separating these varieties will be found in the flower size (1 or 2 mm. larger in var. *modesta*) and flower color (a touch of anthocyanin in var. *lushanensis*). It is interesting to note that the sizes

of mitotic chromosomes in the polyploid var. *lushanensis* were observed to be smaller than those in var. *modesta*.

HYBRIDS

Spontaneous hybridization in the wild is not common in *Lonicera*, even though it can take place very readily under cultivation when certain species which otherwise occupy separate geographical areas are brought together. Fertile progeny and frequent backcrossing may result, and it appears that in parts of the genus, at least, speciation has not been dependent upon the existence of genetical or cytological barriers.

Hybridization has been particularly prevalent in three groups: Section LONICERA and Subsections CYPHEOLAE (Raf.) Rehd. and EUCAPRIFOLIUM (Spach) Rehd. of Subgenus CAPRIFOLIUM. Hybridization between different subsections has frequently taken place, with the production of fertile offspring, and it would seem that they cannot be natural groups.

In order that the possible effects of hybridization on the behavior of the chromosomes could be borne in mind during this investigation, the following list of hybrids has been compiled from the literature. The parental species are arranged alphabetically, and the sequence is that of the first parental species in the classifications of Rehder (1903, 1949).

HYBRIDS OF WILD ORIGIN

LONICERA ALTAICA Pall. × L. PALLASII Ledeb. Recorded by Pojarkova (1958, p. 490); although these species are separated by her in separate series, Ser. *Stenanthae* Pojark. and Ser. *Pallasianae* Pojark. respectively, they are treated by Rehder (1903) as parts of the one variable species, *L. caerulea* L. Pojarkova reports that this hybrid, which is intermediate, occurs near either parent, and also in European USSR, beyond the range of *L. altaica*.

LONICERA HYPOLEUCA Decne. × L. QUINQUELOCULARIS Hardw. According to Wendelbo (1965, p. 15) one of the herbarium sheets of *Lace* 4024 collected at Ziaret, West Pakistan, is a possible hybrid of these two species. If this is so, it is very interesting as representing a cross between species of different sections, Sect. ISIKA and Sect. LONICERA respectively.

LONICERA FLORIBUNDA Boiss. & Buhse × L. NUMMULARIIFOLIA Jaub. & Spach. Recorded by Pojarkova (1958, p. 552) from the western part of Kopet Dag in Turkmenistan; the second parent cited above is treated by Rehder (1903) as a synonym of the wide ranging *L. arborea* Boiss.

LONICERA NUMMULARIIFOLIA Jaub. & Spach × L. QUINQUELOCULARIS Hardw. Wendelbo (1965, p. 15) suggests that the mixture of characters in some plants, where the ranges of distribution of these two species overlap, indicates that introgressive hybridization may be taking place.

LONICERA NIGRA L. × L. XYLOSTEUM L., or L. × HELVETICA Brügger (Jahresber. Naturf. Ges. Graubündens II. 29: 95. 1885 [Mitt. Neue & Krit. Formen der Bündler- & Nachbar-Floren, 50. 1886], Rehder 1903, p.

204). However, Rehder (1927, p. 832) suggests that this "supposed hybrid" is probably a form of *L. xylosteum*.

LONICERA CAPRIFOLIUM L. × L. ETRUSCA Santi, or L. × AMERICANA (Mill.) K. Koch, Wochenschr. Gärtnerei & Pflanzenkunde 10: 279. 1867 (*L. × italica* (Schmidt) Tausch, Flora, 21: 735. 1838).

LONICERA CAPRIFOLIUM L. × L. IMPLEXA Ait. (Rehder 1903, p. 211).

LONICERA CAPRIFOLIUM L. × L. PERICLYMENUM L. (Rehder 1903, p. 212).

LONICERA ETRUSCA Santi × L. IMPLEXA Ait. (Rehder 1903, p. 212).

HYBRIDS OF ORIGIN IN CULTIVATION

LONICERA FRAGRANTISSIMA Lindl. & Paxt. × L. STANDISHII Jacques, or L. × PURPUSII Rehder, Jour. Arnold Arb. 4: 252. 1923.

LONICERA ALPIGENA L. × L. LEDEBOURII Eschsch., or L. × PROPINQUA Zabel, Gartenflora 38: 580. 1889.

LONICERA TATARICA L. × L. XYLOSTEUM L., or L. × XYLOSTEOIDES Tausch, Flora 21: 736. 1838 (*L. × coerulea* Dippel, Handb. Laubh. 1: 233. 1889; Zabel, Mitt. Deutsch. Dendr. Ges. 1901: 94. 1901).

LONICERA KOROLKOWII Stapf × L. TATARICA L., or L. × AMOENA Zabel, Mitt. Deutsch. Dendr. Ges. 1901: 96. 1901.

LONICERA RUPRECHTIANA Regel × L. TATARICA L., or L. × NOTHA Zabel, Gartenflora 38: 525. 1889.

LONICERA MORROWII A. Gray × L. TATARICA L., or L. × BELLA Zabel, *loc. cit.*

LONICERA MORROWII A. Gray × L. RUPRECHTIANA Regel, or L. × MUSCAVIENSIS Rehder, Gartenflora 42: 100. 1893.

LONICERA MORROWII A. Gray × L. × XYLOSTEOIDES Tausch, or L. × MINUTIFLORA Zabel, Gartenflora 38: 523. 1889.

LONICERA × BELLA Zabel × L. RUPRECHTIANA Regel, or L. × MUEN-
DENIENSIS Rehder, Gartenflora 42: 102. 1893.

LONICERA RUPRECHTIANA Regel × L. × XYLOSTEOIDES Tausch, or L. × SALICIFOLIA Dieck ex Zabel, Gartenflora 38: 524. 1889.

LONICERA CHRYSANTHA Turcz. × L. RUPRECHTIANA Regel, or L. × GIBBIFLORA Dippel, Handb. Laubh. 1: 237. 1889, non Maximowicz.

LONICERA CHRYSANTHA Turcz. × L. XYLOSTEUM L., or L. × PSEUDO-
CHRYSANTHA Braun ex Rehder, Man. Cult. Trees & Shrubs 833. 1927.

LONICERA DEFLEXICALYX Batal. × L. QUINQUELOCULARIS Hardw., or L. × VILMORINII Rehder, Mitt. Deutsch. Dendr. Ges. 1912: 194. 1913.

LONICERA FLAVA Sims × L. HIRSUTA Eaton (Rehder 1903, p. 211).

LONICERA FLAVA Sims × L. PROLIFERA (Kirchn.) Rehd. (Zabel in Beis-
sner, Schelle & Zabel, Handb. Laubh.-Benenn. 450. 1903, as *L. flava* ×
sullivantii).

LONICERA HIRSUTA Eaton × L. PROLIFERA (Kirchn.) Rehd., or L. × SARGENTII Rehder, Jour. Arnold Arb. 7: 37. 1926.

LONICERA HIRSUTA Eaton × L. SEMPERVIRENS L., or L. × BROWNII (Regel) Carr. Fl. des Serres, 11: 123. 1856.

LONICERA ETRUSCA Santi \times L. IMPLEXA Ait. (Rehder 1903, p. 212).

LONICERA ETRUSCA Santi \times L. PERICLYMENUM L. (Mottet, Revue Hort. 1900: 695. 1900).

LONICERA DIOICA L. \times L. FLAVA Sims (Rehder 1903, p. 211).

LONICERA DIOICA L. \times L. HIRSUTA Eaton (Zabel in Beissner, Schelle & Zabel, Handb. Laub.-Benenn. 450. 1903 as *L. glauca* Hill \times *L. hirsuta* Eaton).

LONICERA DIOICA L. \times L. PROLIFERA (Kirchn.) Rehd., or L. \times EPSOMIENSIS Hort. ex K. Koch, Dendr. 2(1): 12. 1872, *nomen*.

LONICERA SEMPERVIRENS L. \times L. TRAGOPHYLLA Hemsl., or L. \times TELLMANNIANA Magyar ex Späth, Hauptverz. no. 241. 1927-28 (not seen).

LONICERA CAPRIFOLIUM L. \times L. ETRUSCA Santi, or L. \times AMERICANA K. Koch, Wochenschr. Gärtnerei & Pflanzenkunde 10: 279. 1867. (*L. \times italica* Tausch, Flora 21: 725. 1838).

LONICERA \times AMERICANA K. KOCH \times L. SEMPERVIRENS L., or L. \times HECKROTTII Hort. ex Rehder, in Bailey, Cycl. Amer. Hort. 2: 942. 1900.

In addition, it has been suggested that *Lonicera myrtilloides* Purpus (Mitt. Deutsch. Dendr. Ges. 1907: 255. 1908) might be a hybrid of *L. angustifolium* Wall. \times *L. myrtillus* Hook. f. & Thoms. (see Rehder, Man. Cult. Trees & Shrubs, 822. 1927) and that *L. micranthoides* Zabel (Mitt. Deutsch. Dendr. Ges. 1901: 94. 1901) might be the hybrid *L. nigra* L. \times *L. tatarica* L. (see Rehder, Annual Rep. Missouri Bot. Gard. 14: 204. 1903), but *L. micranthoides* was later treated by Rehder (1927, p. 833) as a probable synonym of *L. \times xylosteoides* Tausch. Likewise, and in the same works, Rehder treated *L. segreziensis* Lavallé ex Dippel (Handb. Laubh. 1: 221. 1889) first as a hybrid of *L. quinquelocularis* Hardw. and *L. xylosteum* L. and later as a probable synonym of *L. xylosteum* L. Rehder (1927, p. 832) also has a note that the supposed hybrid of *L. nigra* L. \times *L. orientalis* Lam. is probably a form of *L. \times xylosteoides*.

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Table. CHROMOSOME NUMBERS IN LONICERA

SPECIES	<i>n</i>	<i>2n</i>	AUTHORITY	DOCUMENTATION AND COLLECTOR	GENERAL DISTRIBUTION
Subgenus LONICERA (Subgen. <i>Chamaecerasus</i> (L.) Rehd.)					
Sect. ISOXYLOSTEUM Rehd.					
Subsect. MICROSTYLAE Rehd.					
<i>L. myrtillus</i> ^a		(18) ^b	7 ^c		Pakistan to Sikkim Himalaya
var. <i>depressa</i>		(36)	7		Himalaya
<i>L. myrtilloides</i>	(9)	(18)	6		? hybrid, <i>L. angustifolia</i> × <i>myrtillus</i>
<i>L. tomentella</i>		(18)	7		Sikkim
<i>L. thibetica</i>	(9, 18)		2		Western China
		(18, 36)	7		
<i>L. rupicola</i>		(18)	7		Himalaya
<i>L. syringantha</i>		(18)	7		Northwest China
Sect. ISIKA (Adans.) Rehd.					
Subsect. PURPURASCENTES Rehd.					
<i>L. microphylla</i> Willd. ex Roem. & Schult.	(18)		2		Central Asia
		(36)	7		
	18		12*	AA ^d 1008-52-B, <i>Dodd & Dudley</i> , 12 May 1965	
<i>L. canadensis</i>		(18)	7		Northeast America
<i>L. tenuipes</i> Nakai	(18)		2		Japan
		(18)	7		
	18	36	12*	AA 11147 (<i>Wilson</i> 6713, Japan, 1914), <i>Dudley & Dodd</i> , 10 May 1965	
Subsect. CAERULEAE Rehd.					
<i>L. caerulea</i> L.	(9, 18)		2		Eurasia
	(9)	(18)	6		
		(18, 36)	7		
	18	36	12*	AA 215-35, <i>Kreps</i> , 25 May 1964	
	18	36	12*	AA 126-37, <i>Kreps</i> , 25 May 1964	
	18	36	12*	AA 20-43, <i>Kreps</i> , 25 May 1964	
	18		12*	AA 808-51, <i>Kobuski &</i> <i>Metcalf</i> , 9 May 1930 (as AA 5300)	
var. <i>edulis</i> Regel	18		12*	AA 6714, <i>Rehder</i> , 7 May 1924	Siberia and Tibet
f. <i>graciliflora</i> Dippel		18	12*	AA 15727, <i>Palmer</i> , 7 May 1921	Turkestan

^a Species names cited without authority are those used in undocumented counts; the sequence of species is that of Rehder (1903, 1949).^b Numbers in parentheses are those given for undocumented counts.^c 1, Vilmorin & Simonet (1927); 2, Sax & Kribs (1930); 3, Matsuura & Suto (1935); 4, Sugiura (1936); 5, Hagerup (1941); 6, Poucques (1949); 7, Janaki Ammal & Saunders (1952); 8, Chuang et al. (1962); 9, Sorsa (1962); 10, Sorsa (1963); 11, Gadella & Kliphuis (1963); 12, Rüdénberg (1964); 12*, Rüdénberg, reported here for the first time.^d AA in the Documentation column indicates that the number which follows is an Arnold Arboretum accession number.

SPECIES	<i>n</i>	<i>2n</i>	AUTHORITY	DOCUMENTATION AND COLLECTOR	GENERAL DISTRIBUTION
Subsect. PILEATAE Rehd. <i>L. gymnochlamydea</i> Hemsl.	9		12*	AA 15032-A (<i>Wilson</i> 266, W. Hupeh, 1908), <i>Green</i> , 27 May 1965	Western China
<i>L. pileata</i>	(9)	(18)	6		Central and western China
<i>L. nitida</i>	(9)	(18)	7		Western China
Subsect. VESICARIAE (Komar.) Rehd. <i>L. vesicaria</i>		(18)	7		Korea
<i>L. ferdinandii</i> Franch.	(9)	(18)	2		Northern China
	(9)	(18)	6		
	9		12*	AA 18360, <i>Palmer</i> , 9 Sept. 1936	
var. <i>induta</i> Rehd.	9	18	12*	AA 18169-A (<i>Purdum</i> 554, Shensi, 1910), <i>Dodd & Callaway</i> , 28 May 1965	
var. <i>leycesterioides</i> (Graebn.) Rehd.		18	12*	AA 5902-A, <i>Kreps</i> , 25 May 1964	Northern China
Subsect. CHLAMYDOCARPI Jaub. & Spach <i>L. iberica</i> M. Bieb.	9		12*	AA 955-1, <i>Rehder</i> ?, 29 June 1916	Transcaucasia and Persia

Subsect. FRAGRANTISSIMAE Rehd. <i>L. standishii</i> Jacques	(9)	(18)	6		China
		(18)	7		
	9		12*	AA 15118-2, <i>Kobuski</i> , 30 Apr. 1932	
f. <i>lancifolia</i> Rehd.	9	18	12*	AA 6669-1-A, <i>Palmer</i> , 31 Mar. 1936 (as AA 6669-1)	
cv. <i>Rosea</i>	9		12*	AA 448-43, <i>Green</i> , 30 Apr. 1964	
<i>L. fragrantissima</i> Lindl. & Paxt.	(9)		2		Eastern China
	(9)	(18)	6		
		(18)	7		
	9	18	12, 12*	AA 2245-1, <i>Rehder</i> , 1 Dec. 1927	
<i>L. × purpusii</i> Rehd.	9	18	12*	AA 397-36-B, <i>Green</i> , 30 Apr. 1964	Cultivation
		18	12*	AA 486-43, <i>Green</i> , 30 Apr. 1964	
Subsect. BRACTEATAE (Hk. f. & Thoms.) Rehd. <i>L. altmannii</i>	(9)		2		Turkestan
		(18)	7		
<i>L. praeflorens</i> Batal.		18	12*	AA 10103-B (<i>Wilson</i> 8441, Japan, 1917), <i>Green</i> , 30 Apr. 1964	Manchuria, Korea and Japan
		18	12*	AA 657-26, <i>Palmer</i> , 25 Mar. 1938	
<i>L. hispida</i>	(9)	(18)	6		Turkestan
var. <i>bracteata</i>		(18)	7		Himalaya to western China

SPECIES	<i>n</i>	<i>2n</i>	AUTHORITY	DOCUMENTATION AND COLLECTOR	GENERAL DISTRIBUTION
<i>L. chaetocarpa</i>		(18)	7		Western China
Subsect. PYRENAICAE Rehd.					
<i>L. pyrenaica</i>		(18)	7		Pyrenees
Subsect. DISTEGIAE (Raf.) Rehd.					
<i>L. involucrata</i> (Richards.) Banks ex Spreng.		(18)	7		Northern America and south into Rocky Mts.
	9	18	12*	AA 16-44, <i>Palmer</i> , 16 July 1936 (as AA 221-33)	
<i>f. humilis</i>		(18)	7		Colorado
<i>f. serotina</i> Koehne	9		12*	AA 817-61, <i>Green</i> , 21 June 1965	Colorado
<i>L. ledebourii</i>		(18)	7		California
Subsect. ALPIGENAE Rehd.					
<i>L. alpigena</i>	(9)	(18)	6		Central and southern European Mts.
		(36)	7		
<i>f. nana</i> (Carr.) Zabel		18	12*	AA 14994-1, <i>Allen</i> , 13 Aug. 1927	
<i>L. glehnii</i>	(9)		6		Japan
		(36)	7		
<i>L. webbiana</i> Wall. ex DC.	18	36	12*	AA 1735-4-B, <i>Green</i> , 20 May 1965	Afghanistan to the Himalaya
<i>L. tatsiensis</i>	(9)		6		Western China

Subsect. RHODANTHAE (Maxim.) Rehd.

<i>L. maximowiczii</i>		(18)	7		Saghalin and Korea
<i>L. subsessilis</i> Rehd.		18	12	AA 11732 (<i>Wilson</i> 9275, Korea, 1917), <i>Rehder</i> , 29 May 1923	Korea
<i>L. orientalis</i> Lam.	(9)		2		Asia Minor to western China
		(18)	7		
		18	12*	AA 417-38-A, <i>Dudley</i> , 4 June 1965	
	9		12*	AA 798-41, <i>Dudley</i> , 4 June 1965	
var. <i>caucasica</i> (Pallas) Rehd.		(18)	7		Transcaucasia, Asia Minor and Persia
	9		12*	AA 15098-1, <i>Rehder</i> ?, 23 June 1916	
	9		12*	AA 364-29, <i>Palmer</i> , 6 June 1940	
var. <i>longifolia</i>		(18)	7		? Kamchatka
<i>L. discolor</i>		(18)	7		Afghanistan to Kashmir
<i>L. modesta</i> Rehd.	9	18	12*	AA 24-36, <i>Green</i> , 31 May 1965	Central China
var. <i>lushanensis</i> Rehd.	18	36	12*	AA 765-36, <i>Green</i> , 31 May 1965	Central China
<i>L. nervosa</i>		(18)	7		Northwest China
<i>L. nigra</i> L.	(9)	(18)	6		Central and southern European Mts.
		18	12*	AA 771-35, <i>Kreps</i> , 25 May 1964	

SPECIES	<i>n</i>	<i>2n</i>	AUTHORITY	DOCUMENTATION AND COLLECTOR	GENERAL DISTRIBUTION
Section LONICERA (Sect. <i>Coeloxylosteum</i> Rehd.)					
Subsect. TATARICAE Rehd.					
<i>L. tatarica</i> L.	(9)		2		Eastern Europe to Turkestan
	(9)	(18)	6		
		(18)	7		
		18	12*	AA 328-39-B, <i>Kreps</i> , 28 May 1964	
		18	12*	AA 287-41-A, <i>Kreps</i> , 25 May 1964	
	9		12*	AA 289-41-A, <i>Green</i> , 31 May 1965	
	9	18	12*	AA 112-42, <i>Green</i> , 20 May 1965	
	9	18	12*	AA 305-51, <i>Kreps</i> , 26 May 1964	
f. <i>angustifolia</i> (Kirchn.) Rehd.	9		12*	AA 4035, <i>Rehder</i> ?, 7 June 1916	
f. <i>elegans</i> Carr.	9		12*	AA 326-39, <i>Kreps</i> , 25 May 1964	
f. <i>fenzlii</i> Dippel	9		12*	AA 306-32, <i>Rehder</i> ?, 21 May & 12 July 1915 (as AA 7337)	
f. <i>grandiflora</i>		(18)	7		
f. <i>latifolia</i>		(18)	7		
f. <i>leroyana</i> (Zabel) Rehd.	9	18	12*	AA 566-57-A, <i>Kreps</i> , 25 May 1964	
f. <i>lutea</i> (Loud.) Rehd.	9		12*	AA 18293, <i>Kobuski</i> & <i>Metcalf</i> , 9 May 1930	
f. <i>punicea</i>		(18)	7		
f. <i>rosea</i> Regel		(18)	7		
	9		12*	AA 7335, <i>Rehder</i> , 21 May & 12 July 1915	
f. <i>roseo-alba</i> Regel		18	12*	AA 15132, <i>Rehder</i> , 21 May & 12 July 1915	
f. <i>sibirica</i> (Pers.) Rehd.		(18)	7		
		18	12*	AA 3771-1-A, <i>Kobuski</i> & <i>Metcalf</i> , 9 May 1930 (as AA 3771-1)	
	9		12*	AA 716-45-A, <i>Kreps</i> , 26 May 1964	
f. <i>virginalis</i> Jaeger	9		12*	AA 199-53, <i>Kreps</i> , 25 May 1964	
cv. Arnold Red	9		12*	AA 243-49 (Type clone), <i>Kreps</i> , 25 May 1964	
cv. Hack's Red		18	12*	AA 475-56, <i>Kreps</i> , 25 May 1964	
cv. Morden Orange	9		12*	AA 306-58, <i>Kreps</i> , 25 May 1964	
cv. Sheridan Red	9		12*	AA 476-56, <i>Kreps</i> , 25 May 1964	
var.	9		12*	AA 791-49, <i>Kreps</i> , 25 May 1964	
cv. (unnamed dwarf)		18	12*	AA 304-58, <i>Kreps</i> , 25 May 1964	
	9	18	12*	AA 302-59, <i>Green</i> , 20 May 1965	

SPECIES	<i>n</i>	<i>2n</i>	AUTHORITY	DOCUMENTATION AND COLLECTOR	GENERAL DISTRIBUTION
<i>L. × xylosteoides</i> Tausch	9		12*	AA 5406, <i>Palmer</i> , 7 July 1936	Cultivation
<i>L. floribunda</i> Boiss. & Buhse	18		12*	AA 341-44, <i>Kreps</i> , 1 June 1964	Northern Persia
<i>L. korolkowii</i> Stapf.	(9)		2		Turkestan, Afghanistan and Pakistan
	9	(18) 18	12*	AA 976-6-A (Type clone), <i>Sargent</i> , 31 May 1891 (as AA 976), and <i>Dudley</i> , 10 July 1965	
var. <i>aurora</i> Koehne		18	12*	AA 10083-B, <i>Dudley</i> , 10 June 1965	
var. <i>floribunda</i> Nicholson	9		12*	AA 20444, <i>Palmer</i> , 8 Sept. 1936	
<i>L. × amoena</i> Zabel (backcross to <i>L. tatarica</i>)	9	(18)	12*	AA 10083-2-A, <i>Palmer</i> , 27 May 1936	Cultivation
		18	12*	AA 818-35, <i>Green</i> , 26 May 1965	
var. <i>arnoldiana</i> Rehd.	9	18	12*	AA 181-44-B, <i>Kreps</i> , 25 May 1964	
f. <i>alba</i> Zabel	9		12*	AA 180-44-A, <i>Kreps</i> , 25 May 1964	
			12*	AA 793-49-A & B, <i>Kreps</i> , 25 May 1964	

Subsect. OCHRANTHAE (Zabel) Rehd. <i>L. ruprechtiana</i> Regel	(9)	(18)	6		Manchuria to northern China
		(18)	7		
	9		12*	AA 15111, <i>Rehder</i> , 19 May 1910	
var. <i>calvescens</i> Rehd.		(18)	7		
	9		12*	AA 15112, <i>Kobuski & Metcalf</i> , 16 May 1930	
f. <i>xanthocarpa</i> (Zabel) Zabel	9		12*	AA 15109-1-B, <i>Rehder</i> , 6 Aug. 1919 (as AA 15109-1)	
	9	18	12*	AA352-62, <i>Kreps</i> , 25 May 1964	
<i>L. × notha</i> Zabel (backcross to <i>L. tatarica</i>)	9		12*	AA 15134-A, <i>Green</i> , 24 May 1965	Cultivation
	9		12*	AA 572-1-A, <i>Palmer</i> , 15 May & 7 July 1936 (as AA 572)	
f. <i>alba</i> Zabel	9		12*	AA 969-4, <i>Palmer</i> , 7 July 1936	
	9		12*	AA 348-32, <i>Kobuski & Metcalf</i> , 16 May 1930 (as AA 3744-1)	
f. <i>carnea</i> Dippel	9		12*	AA 5403, <i>Kobuski & Metcalf</i> , 16 May 1930	
f. <i>carneo-rosea</i> Zabel	9		12*	AA 3743, <i>Palmer</i> , 7 July 1936	

SPECIES	<i>n</i>	<i>2n</i>	AUTHORITY	DOCUMENTATION AND COLLECTOR	GENERAL DISTRIBUTION
<i>L. xylosteum</i> L.	(9)	(18)	6		Europe to Altai Mts.
	(9)		9		
		(18)	7, 10		
	9		12*	AA 15142-A, <i>Dodd & Callaway</i> , 25 June 1965	
	9		12*	AA 422-39, <i>Green</i> , 31 May 1965	
	9		12*	AA 57-42, <i>Kreps</i> , 26 May 1964	
		18	12*	AA 556-51, <i>Kreps</i> , 26 May 1964	
	9		12*	AA 281-53, <i>Green</i> , 31 May 1965	
<i>f. mollis</i>		(18)	7		
cv. <i>Claveyi</i>		18	12*	AA 349-55, <i>Kreps</i> , 25 May 1964	
<i>L. chrysantha</i> Turcz.	(9)		2		Northeast Asia and Japan
		(18)	7		
	9		12*	AA 61-29, <i>Kreps</i> , 25 May 1964	
var. <i>longipes</i> Maxim.		(18)	7		Northwest China
		18	12*	AA 21592 (<i>Rock</i> , S. W. Kansu, 1925), <i>Kreps</i> , 25 May 1964	
	9		12*	AA 558-51, <i>Kreps</i> , 26 May 1964	
<i>f. latifolia</i> Korshinsky	9		12*	AA 15008-2, <i>Kobuski & Allen</i> , 17 May 1933	
<i>f. regeliana</i> (Kirchn.) Rehd.		18	12*	AA 15015, <i>Palmer</i> , 7 May 1921	
<i>f. villosa</i> Hort. ex Rehd.	9		12*	AA 5297-B, <i>Green</i> , 21 July 1965	
<i>L. × pseudo-chrysantha</i>		(18)	7		Cultivation
<i>L. koehneana</i> Rehd.		(18)	7		Western China
	9		12*	AA 5976, <i>Palmer</i> , 10 July 1936	
	9	18	12*	AA 15043 (<i>Wilson 93a</i> , W. Hupeh, 1907) <i>Rehder</i> ?, 29 May 1913	
<i>L. maackii</i> (Rupr.) Maxim.	(9)		2		Manchuria and China
	(9)	(18)	6		
		(18)	7		
	9		12*	AA 15047, <i>Kobuski & Metcalfe</i> , 2 June 1930	
	9		12*	AA 1026-37-A, <i>Green</i> , 21 July 1965	
<i>f. erubescens</i>		(18)	7		
<i>f. podocarpa</i> Franch. ex Rehd.		18	12*	AA 10085-B, <i>Kreps</i> , 25 May 1964	China
<i>L. deflexicalyx</i> Batal.		(18)	7		Western China
		18	12*	AA 6674 (<i>Wilson 4179</i> , Szechuan, 1910), <i>Rehder</i> , 3 June 1918	
<i>L. × vilmorinii</i> Rehd.	9	18	12*	AA 4801-2-B, <i>Green</i> , 21 June 1965	Cultivation

SPECIES	<i>n</i>	<i>2n</i>	AUTHORITY	DOCUMENTATION AND COLLECTOR	GENERAL DISTRIBUTION
<i>L. trichosantha</i>		(18)	7		Western China
<i>f. acutiuscula</i> Rehd.		18	12	AA 15106-1, <i>Palmer</i> , 19 May & 18 Sept. 1936	
<i>L. prostrata</i>	(9)		2		Western China
<i>L. quinquelocularis</i>	(9)		2		Afghanistan to the Himalaya
<i>f. translucens</i> (Carr.) Zabel	(9) 9	(18)	6 12*	AA 5966-2, <i>Rehder</i> , 22 Sept. 1932	
	9		12*	AA 27-33, <i>Palmer</i> , 18 June 1940	
Sect. NINTOOA (Sweet) Maxim.					
Subsect. BREVIFLORAE Rehd.					
<i>L. alseuosmoides</i>	(18)		1, 2		Western China
var. "coriacea" ^e		(36)	7		
<i>L. henryi</i> Hemsl.	(27)	(54)	7		Western China
		(54)	7		
		54	12*	AA 5968-A (<i>Wilson</i> 254, W. Hupeh, 1907), <i>Green</i> , 3 Nov. 1965	
Subsect. LONGIFLORAE Rehd.					
<i>L. biflora</i>		(18)	7		Southern Europe and northeast- ern Africa
Subgenus CAPRIFOLIUM (Adans.) Dippel (Subgen. <i>Periclymenum</i> (Mill.) Rehd.)					
Subsect. PHENIANTHI (Raf.) Rehd.					
<i>L. sempervirens</i> L.	(9)	(18)	6		Eastern and central North America
		(18)	3		
		36	12*	AA 771-57-B, <i>Dodd &</i> <i>Callaway</i> , 4 June 1965	
cv. Dreer's Everblooming	18		12*	AA 745-60, <i>Dudley</i> , 30 July 1964	
cv. Magnifica	18		12*	AA 543-61, <i>Dudley</i> , 30 July 1964	
<i>L. × tellmanniana</i> Magyar ex Späth		(ca. 45)	7		Cultivation
Subsect. CYPHEOLAE (Raf.) Rehd.					
<i>L. yunnanensis</i>		(18)	7		Southwestern China
<i>L. dioica</i> L.	(9)		2		Eastern North America
		18	12*	AA 130-49, <i>Kreps</i> , 1 June 1964	
<i>L. prolifera</i>	(9)		2		Central North America
		(18)	7		

^e No such variety has been traced, it is suspected that this may have been an error for *L. henryi* Hemsl. var. *subcoriacea* Rehd.

SPECIES	<i>n</i>	<i>2n</i>	AUTHORITY	DOCUMENTATION AND COLLECTOR	GENERAL DISTRIBUTION
<i>L. flava</i> Sims	9		12*	<i>C. E. Wood, Jr.</i> 8919, Walker Co., Georgia (A); AA 557-59, a clonal propagation from this collection	Eastern North America
		18	12*	<i>C. E. Wood, Jr.</i> 8963, DeKalb Co., Alabama (A); AA 556-59, a clonal propagation from this collection, <i>Green</i> , 31 May 1965	
Subsect. EUCAPRIFOLIA (Spach) Rehd.					
<i>L. implexa</i>		(18)	7		Mediterranean
<i>L. caprifolium</i>	(9)	(18)	6		Europe and western Asia
		(18)	7		
<i>L. × americana</i> (Mill.) K. Koch	9	(18)	7		Cultivation
			12*	AA 18-43-B, <i>Dodd &</i> <i>Callaway</i> , 4 June 1965	
<i>L. stabiana</i>	(9)		1		Italy
<i>L. splendida</i>		(18)	7		Spain
<i>L. etrusca</i> Santi		(18)	7		Mediterranean
	9	18	12*	AA 231-46, <i>Dodd &</i> <i>Callaway</i> , 4 June 1965	
<i>L. periclymenum</i> L.	(18?)		5		Europe, western Asia and northern Africa
	(18)	(36)	6		
		(18, 36)	7		
		54	11	<i>Gadella & Kliphuis</i> 534, 623, & 715 (v) [not seen]	
f. <i>belgica</i>		(36)	7		
cv. <i>Wisleyensis</i>		(36)	7		
		Unidentified			
<i>Lonicera</i> sp.	(36)		3		

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ANATOMY OF THE PALM RHAPIS EXCELSA II. RHIZOME¹

P. B. TOMLINSON AND MARTIN H. ZIMMERMANN

THE PALM *Rhapis excelsa* develops horizontal, subterranean rhizomes which bear only non-assimilating scales. This kind of axis may be contrasted with that of some other palms like *Nypa* or *Sabal minor* in which the foliage leaves are borne directly by the underground stem. Scale-leaf bearing rhizomes of the *Rhapis* type are relatively rare in the Palmae (Tomlinson, 1961) although common in other monocotyledonous orders (e.g., Scitamineae, Liliiflorae).

Anatomical comparison of the scale-leaf bearing rhizome with the aërial axis which bears the assimilating foliage is of considerable interest because the two types are morphologically equivalent but their development must be quite different from a nutritional point of view. The present paper is an account of the vascular structure of the mature rhizome. The development of the two types of axes will be described in a later paper in this series.

Palms show two major growth forms. In one kind the vegetative axis is unbranched, producing solitary columnar stems, as in the coconut, in the other it is caespitose by the production of axillary vegetative axes, as in the date. Branching of the second type is always restricted to the base of the parent axis for simple adaptive reasons which are well known (Tomlinson, 1964). Normally these basal suckers rapidly turn erect. The first leaves produced by lateral branches are reduced to scales, but there is a rapid transition to normal assimilating foliage leaves as the branch assumes a vertical position. Thus the construction of the parent axis is repeated and by further branching of all axes a tufted and congested sympodial system results. *Rhapis* represents a growth form in which mutual competition of successive segments of the sympodium is eliminated by long-continued horizontal growth of the branch before it turns erect (FIG. 1A). The rhizome in *Rhapis* is essentially the early stage of sucker development which has become much protracted. In some ways it is a "persistently juvenile" stage of axis development.

MORPHOLOGY OF THE RHAPIS RHIZOME

Axillary shoots which grow out as rhizomes appear in the seedling² of *Rhapis*. After a variable period of horizontal growth the rhizome apex turns

¹ Research on the anatomy of palms by P. B. Tomlinson is supported by National Science Foundation Grant GB 2991.

² Seedling morphology and anatomy will be described in a subsequent paper.

erect and there is a rapid period of transitional growth leading to the establishment of an erect leafy shoot. Features of the construction and growth of rhizome segments are shown in FIGS. 1 and 2. In the transitional period of growth the axis is somewhat swollen (FIGS. 2B, C, D, 1B) and successive leaves are elaborated so that a transition between the scale leaves of the rhizome (FIG. 1C) and the foliage leaves of the aërial stem occurs (FIGS. 1D-F). Transitional leaves show a gradual development of the blade which may be initially either compound or simple depending on the vigor of the shoot. Only compound leaves are illustrated in FIG. 1D-F. This transitional sequence clearly illustrates that the scale leaf is morphologically equivalent to the base of the adult foliage leaf.

The sympodium is continued by new rhizomes originating as buds in the axils of scale or transitional leaves at the base of the newly-erect shoot

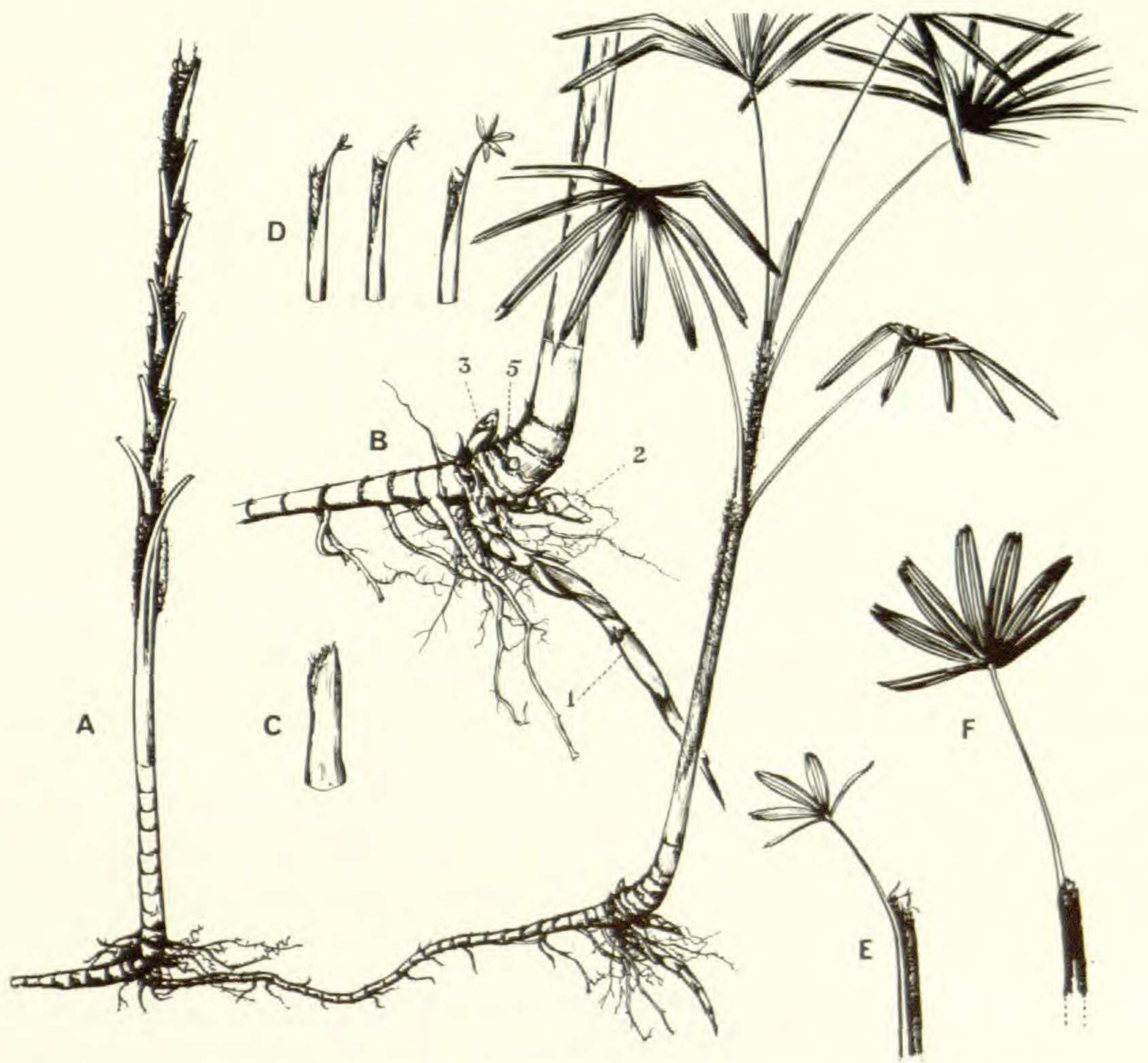


FIGURE 1. Relation of aërial to underground axes in *Rhapsis excelsa*. A. One segment of sympodium, foliage leaves removed from aërial shoot at left, $\times 1/8$. B. Base of right-hand aërial shoot of FIG. 1A, all but distal leaves removed, $\times 1/4$. Numbers 1-5 refer to renewal shoots of successive age, youngest distal, oldest proximal, number 4 is on the remote side of the axis. C. Scale leaf from rhizome, $\times 1/2$. D-F. Successive leaves from transitional sequence at base of erect shoot, $\times 1/4$, showing gradual development of blade. Adult foliage leaves have blades 4-5 times wider than that of leaf illustrated in FIG. 1F.

(FIG. 2D). Several buds may grow out, in the order of their age (FIG. 1B) and in this way the sympodium multiplies. With frequent production of laterals sympodia may become very complex (FIG. 2E). Clonal spread of *Rhapis* under favorable conditions is therefore rapid. Erection of rhizome

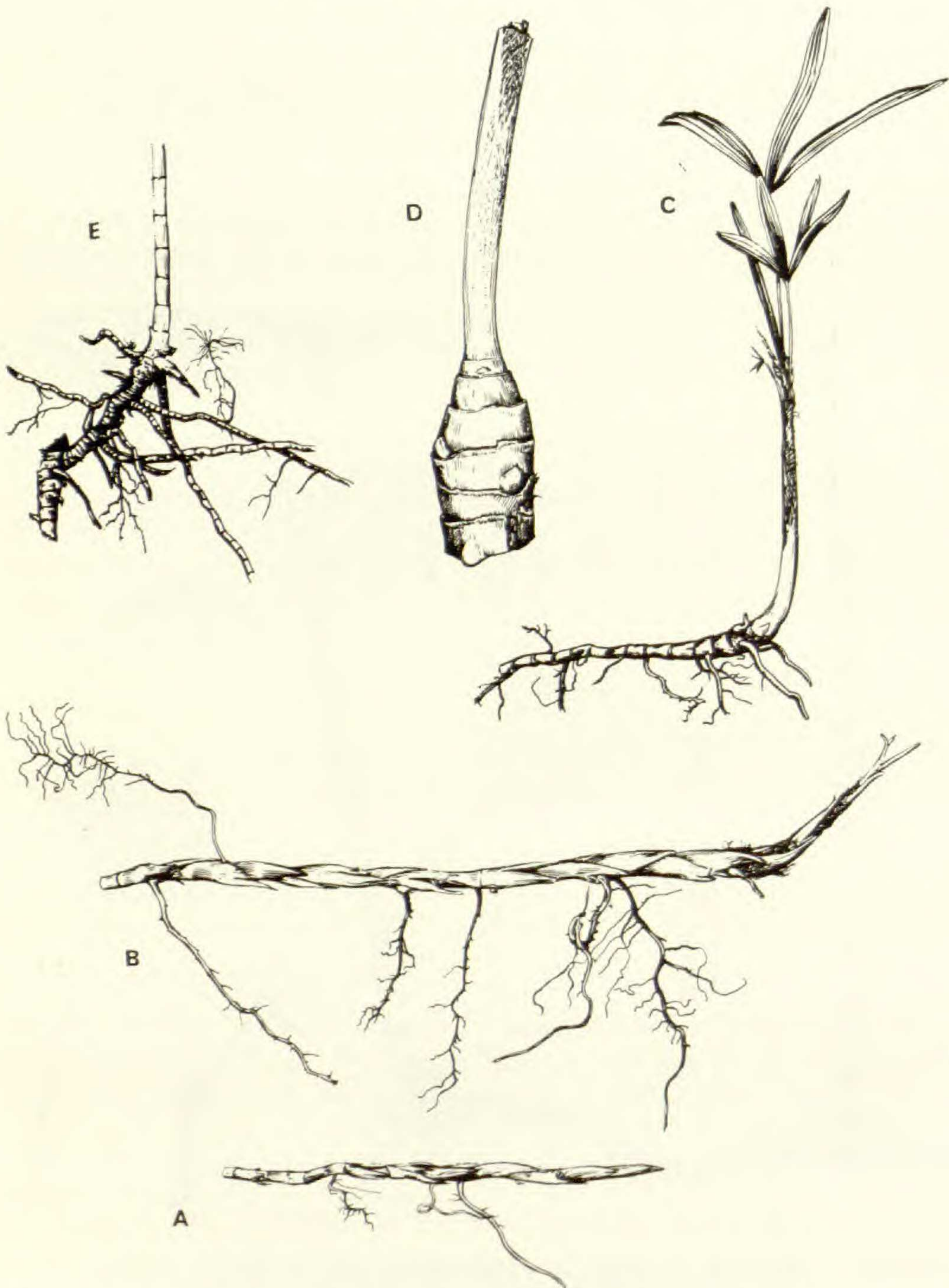


FIGURE 2. Development of rhizome system in *Rhapis excelsa*. A. Apex of underground creeping rhizome, $\times 1/4$. B. Apex of rhizome becoming erect; transitional type of foliage initiated, $\times 1/4$. C. Later stage, transitional leaves with well-developed blades, $\times 1/6$. D. Base of erect shoot at a stage of development corresponding to FIG. 2C; leaves removed to show buds of renewal shoots, $\times 1/2$. E. Old, much-branched rhizome complex, $\times 1/8$.

apices and the morphological responses it induces seem independent of the season in South Florida since all stages of development can be found at any time of year.

Horizontal, underground parts of the rhizome, with which this article is concerned, may be up to 1 meter long and 1 to 1.5 cm. in diameter; the apex is protected by the rigid overlapping scales (FIG. 2A). Scales, like the foliage leaves of the aërial stem, are arranged in a $2/5$ phyllotactic spiral. Each originates as a closed tube with a narrow distal opening which is widened by enlargement of enclosed organs (FIG. 1C). Internodes are 1.5 to 2 cm. long in older parts of the rhizome. The covering of scale leaves is retained for a long time (FIG. 2B). Very old rhizomes still bear the fibrous remains of decayed scales. Neither buds nor their vestiges are associated with scale leaves; they are restricted to the transition region where the rhizome turns erect (FIG. 2D). Roots are borne all around the rhizome at irregular intervals. We have not recorded this quantitatively but it seems to us that root insertions are associated (a) with each other and (b) less obviously, with the nodes. Root production is also vigorous on the swollen regions at the junction of successive sympodium segments. Rhizomes are always colorless and non-assimilating.

MATERIALS AND METHODS

Rhizome segments used in this investigation are all from specimens cultivated at Fairchild Tropical Garden. Sequential sections 30–50 μ thick were cut at 0.5 mm. intervals, stained and mounted by procedures previously described (Zimmermann & Tomlinson, 1965). In order to clarify the vascular system, starch was eliminated from the tissue by immersing sections for 5 to 10 minutes in 50 per cent hydrochloric acid prior to washing and bleaching. For details of nodal anatomy a continuous series of sections from a short length of rhizome was prepared.

Cinematographic analysis was carried out with the drawing method described before (Zimmermann & Tomlinson, 1965) as well as with the optical shuttle (Zimmermann & Tomlinson, 1966). The optical shuttle was also very useful in making quantitative plots of single vascular bundles of the types illustrated in FIG. 4.

In addition to microscopic analysis we have studied the rhizome structure extensively by macro-cinematography of cut surfaces on the microtome. A special clamp for the 'Reichert' sliding microtome was designed and constructed which allows continuous advance of long specimens. Such motion picture sequences give an excellent over-all view of the vascular system.

GENERAL RHIZOME ANATOMY OF RHAPIS

An over-all view of a transverse section of the rhizome is given in FIG. 3.

Rhizome 1–1.5 cm. in diameter, divided into cortex 1–1.5 mm., central

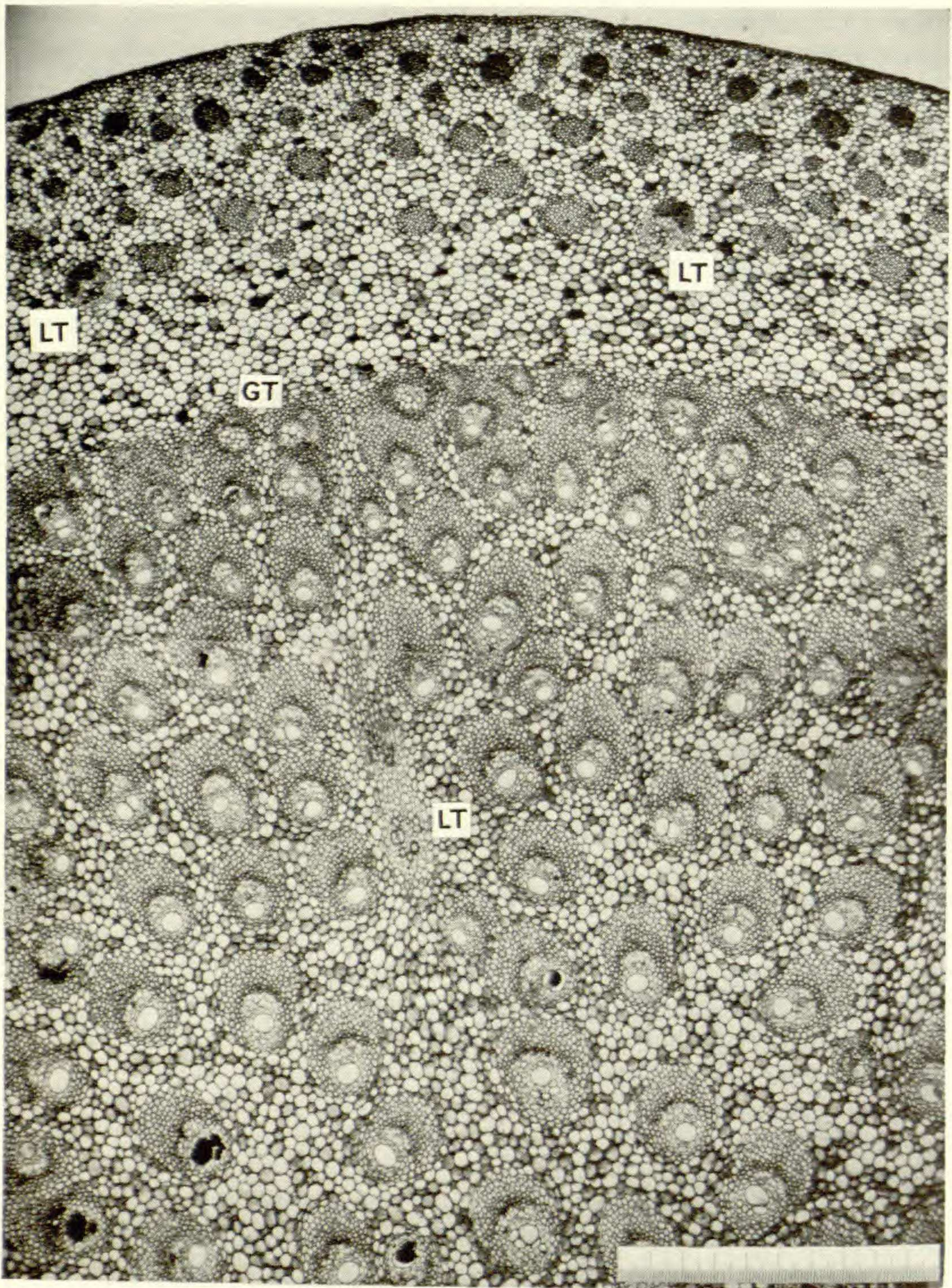


FIGURE 3. *Rhaps excelsa*, transverse section of rhizome. Major leaf trace (LT) to next node above level of section shown in center of figure; two minor leaf traces (LT) to same node shown in cortex. Peripheral girdling traces (GT) are ultimate endings of root traces. Black deposits in lower left-hand corner are tannins. Scale equals 1 mm.

cylinder 8-14 mm. wide. Epidermis uniform, cells elongated, rectangular in surface view with transverse end walls or frequently somewhat spindle-shaped with oblique end walls. Outer epidermal wall thickened, uniformly cutinized.

occasional cells with pronounced pitted thick secondary walls becoming lignified. Stomata not infrequent, resembling those of aërial stem but without chloroplasts and presumably non-functional. Periderm not developed except locally around wounds and leaf scars by ligno-suberisation of ground parenchyma accompanied by divisions of "etagen" type.

Cortex with 3-4 outermost layers of narrow cells with truncate end walls; walls thickened and becoming ligno-suberized to form a narrow hypodermal sclerotic layer interrupted below stomata by loose, wide unligified cells continuous with middle cortex. Middle and inner cortical ground parenchyma with a well-developed intercellular space system, cells frequently becoming slightly thickened and prominently pitted with age. Cortex (FIG. 6), apart from inconspicuous transient leaf traces, including a series of purely fibrous strands, peripheral strands usually narrower than central; largest fibrous strands (up to 120 μ wide) including a narrow central strand of vascular tissue, often only phloem. Innermost cortical layers usually free of fibrous bundles.

Central cylinder not delimited from cortex by endodermis or other specialized layer, but by abrupt transition to narrow compact ground parenchyma with slightly thickened walls and zone of narrow, somewhat congested peripheral vascular bundles. Compact peripheral zone only interrupted by parenchyma at exit of leaf traces to form distinct "leaftrace gaps" (FIG. 6). Central vascular bundles wider, more diffuse. Central ground parenchyma very uniform, cells somewhat wider and looser than those at periphery. Individual vascular bundles of central cylinder more or less completely sheathed by fibrous tissue, but fibers least well developed around xylem. Fibers narrowest and most heavily lignified next to phloem. Peripheral vascular bundles somewhat more fibrous than central, but difference much less pronounced than in aërial stem. Vascular tissues including usually one wide metaxylem vessel and often protoxylem in varying amounts (see below). Phloem strand narrow, uniform, never with a distinct median sclerotic isthmus as is common in bundles of aërial stem. Metaxylem vessel elements average 60 μ wide, 1-1.5 mm. long with oblique or slightly oblique scalariformly perforated end walls with 6-10 thickening bars. Sieve-tubes average 15 μ wide with compound sieve-plates on slightly oblique end walls. Starch abundant in ground parenchyma except for narrow starch-free zone in outer cortex; grains either solitary, more or less spherical or more usually compound, angular. Tannin abundant as dark-brown deposits in otherwise unmodified parenchyma cells in all parts. Vascular tissues commonly occluded by tanniferous deposits giving a strong positive lignin reaction with phloroglucinol and concentrated HCl; tannin occlusions not especially restricted to traces to old leaves. Stegmata (silica cells) only observed next to cortical fibrous bundles. Raphide sacs not observed.

In summary, the general anatomy of the rhizome, as seen in a single transverse section, differs from the aërial stem as follows: relatively greater development of cortex and cortical fibrous system; central and peripheral vascular bundles of central cylinder less conspicuously different; less obvious variation in the numbers of metaxylem elements.

COURSE OF VASCULAR BUNDLES IN THE RHIZOME

Central system. In spite of frequent root insertions the over-all course of vascular bundles in the *Rhapis* rhizome remains quite clear. It resembles

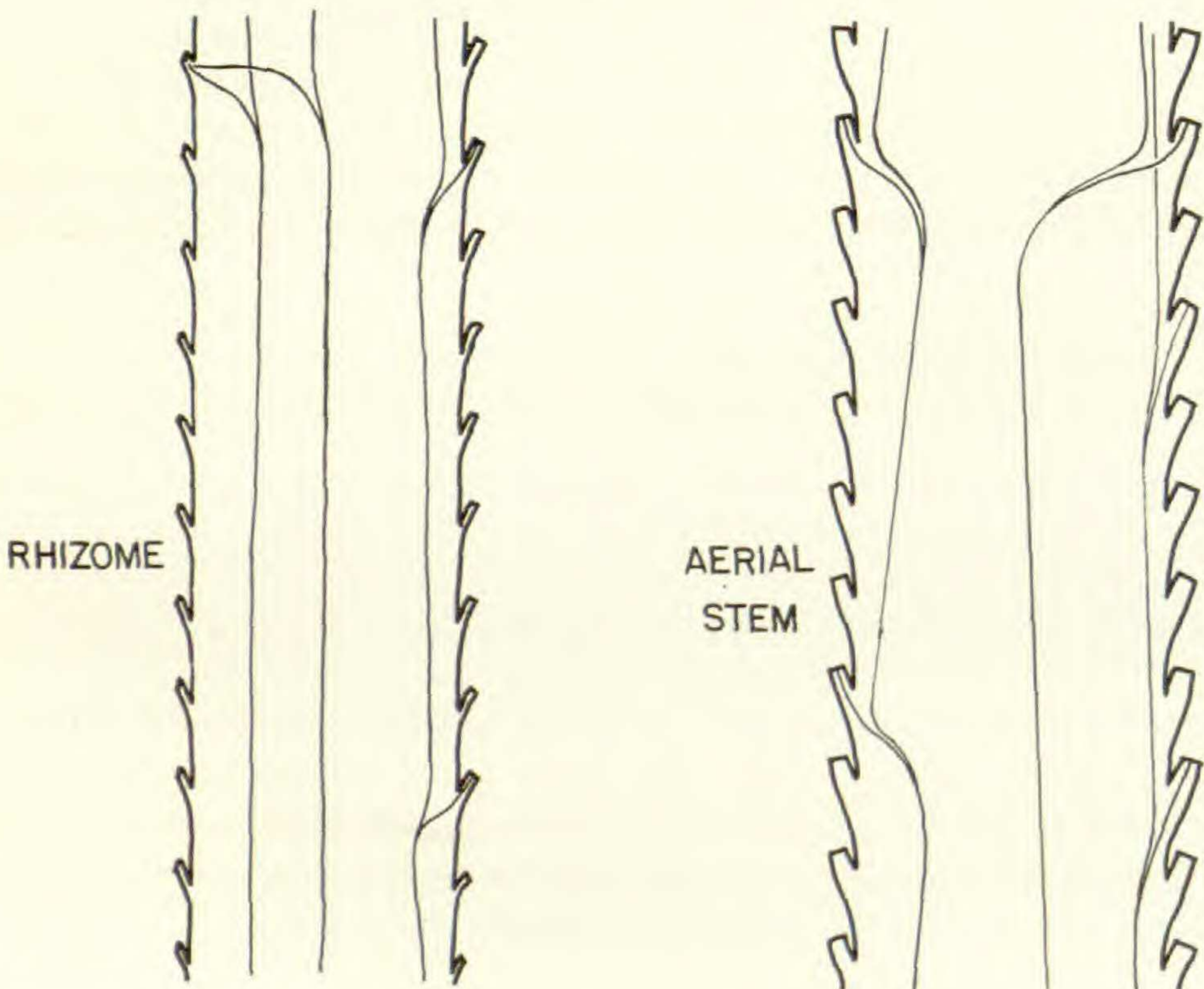
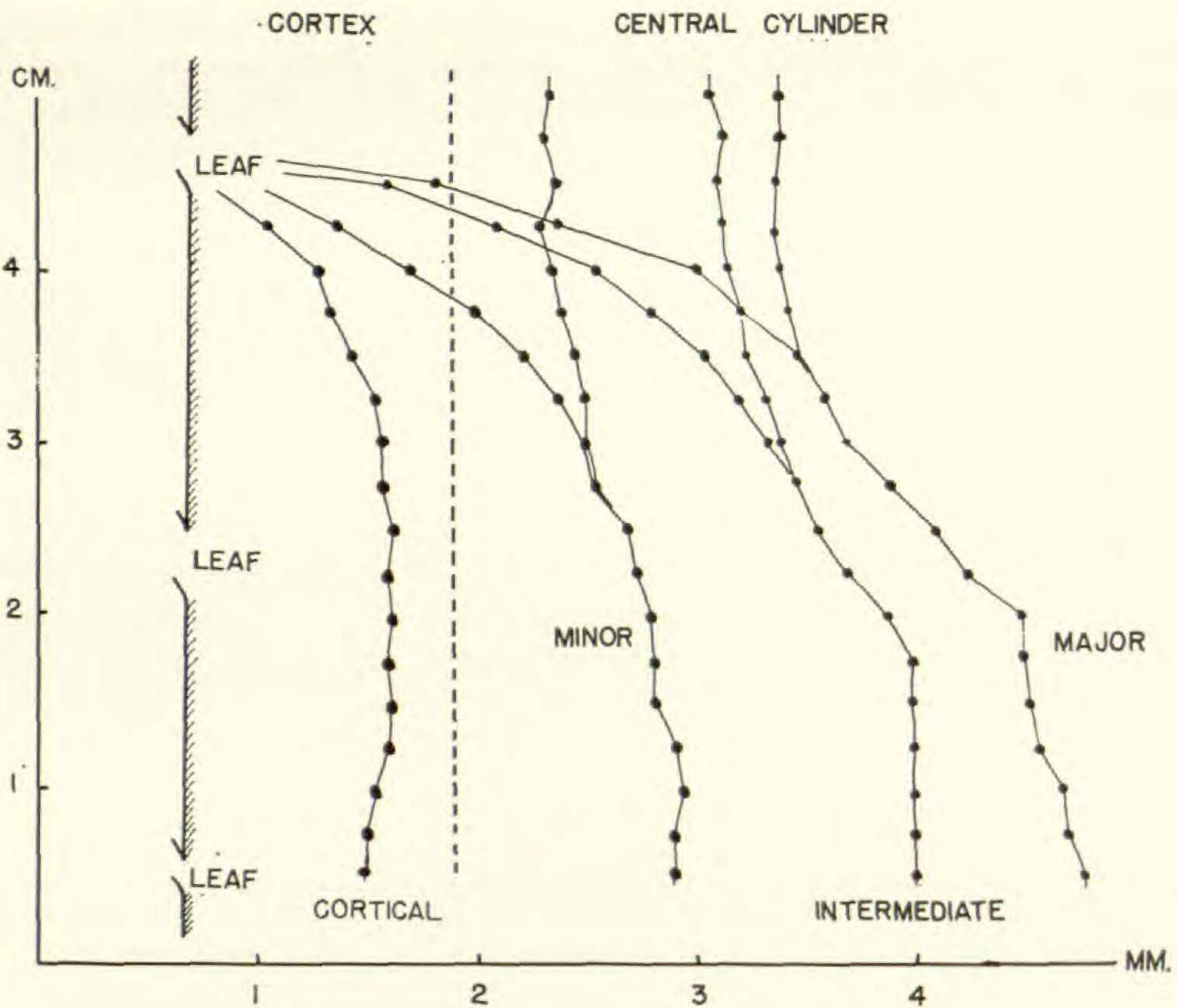


FIGURE 4. ABOVE: plots of vascular bundles supplying scale leaf of rhizome. Measurements taken from microtome sections. Course of major, intermediate, and minor bundles from central cylinder, with continuing vertical bundles, and a cortical bundle without a continuing vertical bundle. The figure is diagram-

the aërial stem and may be described in the same terms. Vascular bundles behave essentially alike, maintaining their individuality throughout the stem. At irregular intervals each of these *vertical bundles*³ forks to give off a *leaf trace* which passes sharply outward into a scale leaf, the vertical bundle continuing distally, eventually to repeat the cycle. Each leaf receives a few branches from the central bundles (*major bundles*) which pass primarily to the dorsal side of the leaf, a larger number of branches from sub-peripheral bundles (*intermediate bundles*), and the largest number of branches from peripheral bundles (*minor bundles*) which pass to all parts of the leaf. There is a continuous series from major (dorsal) to minor (ventral) leaf traces around the stem circumference at each node. Major bundles pass into the leaf much more abruptly than minor bundles (FIG. 4); they may sometimes be horizontal or even pass below the horizontal and are commonly sinuous so that different parts of the same leaf trace occur in a single section. Part of this unevenness is due to the oblique insertion of most scale leaves.

The most significant way in which rhizome bundles differ from those of the aërial stem in over-all distribution is that rhizome bundles deviate from the vertical at points of leaf contact much less than in the aërial stem. Von Mohl's classic "double curve" which is so characteristic of the vascular bundles of aërial stems of palms is therefore not so obvious in the rhizome (FIG. 4 below). Likewise the central bundles of the rhizome do not describe a regular helical path as is common in the aërial stem.⁴ A slight movement does, however, tend to occur in one direction, suggesting an incipient helix.

As in the aërial stem, departure of the leaf trace is complicated by the presence of *bridges* which link it with adjacent vertical bundles, always in an upward direction (FIG. 5D). One to four (usually two) bridges are developed by each leaf trace. Narrow bridges may contain only phloem; the narrowest are sometimes fibrous strands without vascular tissue. Most bridges are short, 2 to 6 millimeters long, but occasionally there are much longer ones resembling vertical bundles until they fuse distally. The significance of this is discussed below. Satellites, which in the aërial stem irrigate inflorescences (or their aborted vestiges), are absent from the rhizome which wholly lacks this lateral type of appendage.

Brief mention may be made of irregular *girdling traces* (FIG. 6 GT)

³ Vertical bundles of the rhizome run horizontally, of course, but the term is used because they are homologous with the vertical bundles of the aërial axis.

⁴ More recent observation of the aërial stem of *Rhapis* has revealed that this internal helix is correlated with phyllotaxis; stems with a right-handed phyllotactic spiral have a right-handed internal helix and vice versa.

matic in that the bundles are all represented in one plane, in fact they enter the leaf along different, widely divergent radii. Dotted vertical line represents limit between cortex and central cylinder, arbitrarily chosen as a base line in making measurements. Horizontal exaggeration 12.5 times.

BELOW: diagrammatic comparison of course of vascular bundles in rhizome and aërial stem (latter figure taken from Zimmermann & Tomlinson, 1965). For comparative purposes the horizontal rhizome is represented in an erect position.

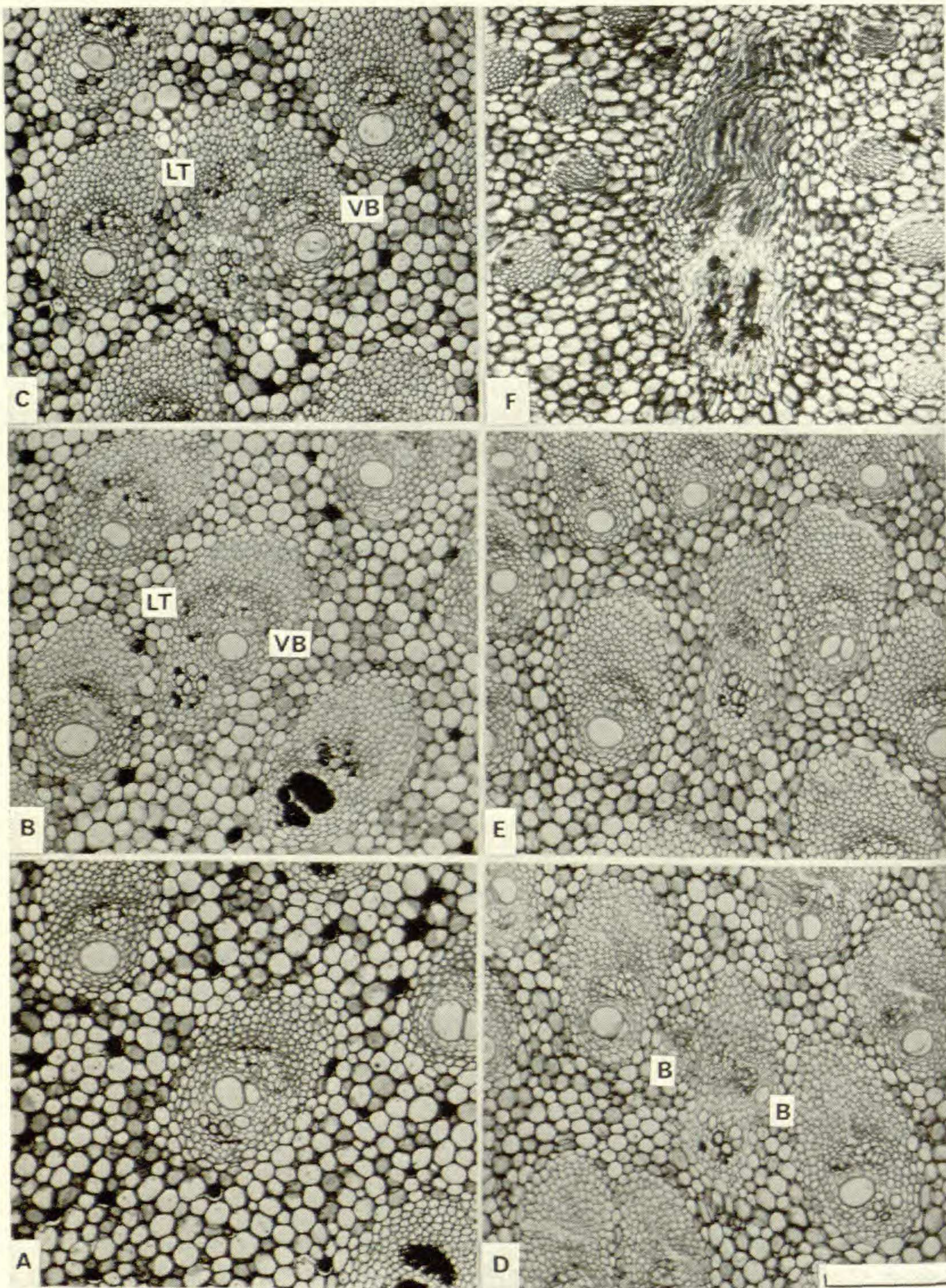


FIGURE 5. Successive transverse sections of the same leaf trace complex from rhizome of *Rhaps excelsa*. In all figures the cortex is towards the upper, the central cylinder towards the lower margin of the plate. Scale is 250μ . A. Vascular bundle in uncrowded central part of stem, below level of forking and with well-developed protoxylem. B. Vertical bundle (VB) to right splitting from leaf trace (LT) at left; 1.85 cm. above A. C. Vertical bundle (VB) at right including one wide metaxylem vessel, no protoxylem, free of leaf trace (LT) at left with no wide metaxylem elements; 2.25 cm. above A. D. Leaf trace further towards cortex splitting off bridges (B) to left and right; vertical bundle is now left behind and is no longer associated with leaf trace; 2.9 cm. above A.